THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[FOURTH SERIES.]

No. 5. MAY 1868.

XXXIX.—*Contributions toward the formation of a correct System of Muscular Homologies.* By ALEXANDER MACALISTER, M.D., L.R.C.S., L.K.Q.C.P., Demonstrator of Anatomy, Royal College of Surgeons, Ireland, one of the Honorary Secretaries of the Royal Geological Society of Ireland *.

THE literature of comparative anatomy is teeming with memoirs and essays on that department of homology which treats of the serial comparison of the muscles of the fore and hind extremities in vertebrate animals.

Almost every writer has originated an hypothesis of his own (some of these being plausible and some fanciful), starting from which he proceeds to work out details, some of which in all theories are undoubtedly true; but every author has differed from his predecessors and successors in his reading of these serial homologies. In the majority of these theories muscular peculiarities have been regarded as subsidiary to osseous arrangements, and many authors have deduced their ideas of homotypical myology from the study of bones rather than from the direct consideration of the muscles themselves and of their relative positions, courses, and attachments. Such being the present position of this branch of comparative anatomy, no apology is needed for bringing forward any observations which may perhaps have the advantage of novelty, and which may elucidate in some degree the vexed question of serial homologies. A great number of the misapprehensions into which anatomists have fallen with respect to these homologies are due to the fact that the individual components of the fore limb of a limited number of animals have been compared directly with those of the hind extremity, irrespective of the differences of the work to which they may be devoted; but this is a mistake in principle, and one from which we may free ourselves by

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regarding the two limbs not immediately as being representatives the one of the other, but as different expressions of a certain type limb, to some extent ideal because not found as an unmodified entity in any animal, but upon whose basis every vertebrate limb is constructed; and apprehending this, we should compare the individual limb before us with the corresponding part of the type extremity,—just as in the science of botany we learn that the various parts of the flower (sepal, petal, stamen, and carpel) are modifications, not of the leaf as Goethe taught, but of a certain ideal organism or phyton, of which the leaf itself is only a variety.

As the study of comparative osteology leads us to the conclusion that there is a typical skeleton, of which all vertebrate skeletons are modifications, so the study of myology teaches us that there is a typical vertebrate *myozoon**, of which the individual vertebrate muscular systems are modifications.

Adopting the theory of a myozoon, the main point of our inquiry resolves itself into a determination of the nature and components of the typical limb; and in our researches we shall commence with such portions as present us with the most clear and constant uniformities of arrangement, and consequently with the fewest difficulties. Thus we will, in the first place, endeavour to resolve into their typical positions the muscles of the terminal segment of the vertebrate limb—the pes or the manus.

There is no primary difficulty in deciding the landmarks in this segment: the pollex and hallux, the little toe and little finger, the carpus and tarsus are undoubtedly correspondent; and the latter may be arranged as follows into a tabular series whose resemblances are evident :—

Scaphoid	= os naviculare pedis.
Semilunar	= astragalus (body).
Cuneiform	= calcaneum.
Pisiform	= sesamoid bone in the long peroneal tendon.
Trapezium	= entocuneiform.
Trapezoid	= mesocuneiform.
Os magnum	
(body)	= ectocuneiform.
(head)	= astragalus (head).
Unciform	= cuboid.

Of the five digits typically present there are two which ge-

* I should, perhaps, apologize for attempting to intrude a new name upon an already name-encumbered science; but I think any new word may be admitted whose meaning is easily understood, when it saves us the trouble of circumlocution. *Myozoon* = *μῦς ζῶον*, muscle animal.

nerally exhibit an individuality of action separate from the others: these are the inner and the outer. For these we have what at first sight appear as separate special muscles often present; but, as Meckel remarked, these can be resolved into the ordinary and typical series which we have developed for the others, only in a position of greater specialization.

Discarding for the present the longer digital muscles, we can resolve the muscles of the pes and manus into the following:—

1. A short extensor for the fingers or toes.
2. A short flexor for the fingers or toes.
3. A complete series of palmar interossei.
4. A complete series of dorsal interossei.

The first of these muscles is developed on the dorsum of the human foot, and is there attached to the four inner toes; only, however, in the case of the great toe is its typical insertion into the first phalanx preserved, as in the three other digits its tendon is confluent with that of the long extensor. It is not usually inserted into the little toe; but I have once seen this muscle in man sending a fifth tendon to that organ. In the manus of man a corresponding muscle occurs as an anomaly occasionally, and as such has been described by Mr. Wood (Proc. Royal Soc. 1865, p. 382) and by myself (Proc. Royal Irish Acad. April 1867); when present, it is often inserted, fleshy or tendinous, not directly into the fingers, but into the extensor longus tendons. This muscle is of rare occurrence in the normal anatomy of lower animals; to my knowledge it is only described as present in the *Bradypus tridactyla*, according to Meckel; and the same writer describes a corresponding muscle arising from the lower end of the ulna in the two-toed Anteater. The comparative anatomy of this muscle in the pes exhibits but little variety; it is present in *Ornithorhynchus*, *Hyrax*, *Myrmecophaga*, *Macropus*, *Arctomys*, Bear, *Nasua*, *Pteropus*, *Rhinolophus*, *Stenops*, *Macacus*, *Ateles*, *Cebus*, *Callithrix*, *Cercopithecus*, Ai, *Hystrix*, and many other animals, in different degrees of perfection, but never varying to any great extent from its usual place.

The second of these muscles may be looked upon as the antithesis of the short extensor: it is the short flexor of the toes and fingers. If we compare the actions of flexion and extension of the digits, we shall find at once that, usually, the latter is provided for by the great development of large and long muscles arising in the forearm. On account of this the flexor of the first phalanx is not usually needed in this its primary capacity; and consequently we find it split up or mo-

dified in several singular ways. As we saw that its antithesis, the extensor, was sometimes inserted, not into the bones directly, but into the common extensor tendon, so we usually see, as in the human pes, part of this flexor arising from the first row of the tarsus, and inserted, as the musculus accessorius, into the tendon of the flexor digitorum longus. And as, from the hyperdevelopment of the calcaneum, the latter tendon is forced to run obliquely to its insertion in the human and some other pedes, so this muscle is adapted in such cases to fulfil the special function of obviating what would otherwise be the faulty direction of the long tendon, and altering its line of action into one of greater convenience: for this purpose the muscle is shortened, or at least its belly is tacked on to the flexor tendons near to the ankle. But the muscle does not terminate here; for, separated from the typical origin by the tendons to which the latter has contracted an adhesion, the continued slips of insertion sink into the interspaces of the tendons, and thence are inserted into the fingers under the name of lumbricales. Within the present session I have seen several distinct examples of the continuity which sometimes subsists in the human foot between the lumbricales and the massa carnea accessoria. In other animals we find the musculus accessorius, varied to a slight extent in direction: it is present in *Ateles*, *Cebus*, and other monkeys. This massa carnea Sylvii, however, is not all of this short flexor; there is one slip which usually preserves its natural connexions—the superficial head of the flexor brevis pollicis manus. It is a typical portion of the muscle, arising from the carpus and inserted into the first phalanx of the pollex through the intervention of the outer sesamoid bone; and this leads us to the consideration of this muscle as developed in the manus. In *Hyrax capensis*, according to Drs. Mivart and Murie (Proc. Zool. Soc. 1865, p. 341), the muscle is present as a flexor brevis digitorum manus, sending slips to the second, fourth, and fifth digits, the slips arising by a large muscular belly in the vicinity of the palmar cartilage; in this case the muscle is developed typically. It may seem as an *à priori* difficulty that this animal has two lumbricales (although Meckel denies their existence) as well as the large typical flexor; but this in reality can easily be understood, as the former are but deeper and differentiated slips of the muscle, just as in the antagonistic foot-muscle, the extensor brevis, I found on a recent occasion two tendons, distributed one to the outer and the other to the inner side of the second toe, all the others being regular. The lumbricales described by the above authors in *Hyrax* are distributed to the second and fourth toes in the fore limb, but to the second and

third in the left foot; of these the second, as indicated in the foot, is evidently the missing third-toe muscle, while the first may be the first-toe muscle, which is not otherwise developed. If this be the case, the matter is still more clearly explicable in accordance with the type proposed above. In *Dasyprocta* the same authors speak of a palmaris brevis muscle attached to the palmar ossicle, but not connected with the digits, arising from the first and fifth metacarpal bones. This muscle is a backward prolongation of the type muscle, and evidently represents the accessorius of the foot; it is not present in the hare or rabbit, but in the guineapig it is distinctly traceable. A small muscle invests the flexor tendons still further forward in *Agouti*, similar to the flexor brevis manus, but which has no separate digital insertion; from the tendons themselves spring the lumbricales, three in number, as in the cavy, guineapig, rabbit, and hare: thus these three severed portions, if united, would constitute an accurate and typical flexor muscle of this series. In the human hand we find that this muscle, losing its bony origin, is connected to the palmar fascia on the inner side, and is known by the name of palmaris brevis, while its digital slips remain as the lumbricales. I have seen this muscle springing from the pisiform bone. Having thus traced this flexor series through its various mutations, we see that, despite its variability of form, it presents a constancy in its presence, and is sometimes developed in a high degree of complexity—for instance, in *Nycticebus* and the Lemuridæ in general, according to the illustrations of Messrs. Mivart and Murie, and the text of Meckel, Vrolik, and others. We find in these animals:—first, a double set of ordinary lumbricales, one on each side of each finger; secondly, an accessory set, likewise in duplicate; and, lastly, a third series, passing from the second to the third phalange of each digit: there are thus, as Meckel states, twenty-four muscles in all of this lumbrical group; of these the first and second groups are only highly differentiated slips of the flexor brevis manus, while the last set may be continuations of the true dorsal interossei.

The next groups of muscles in this segment are the interossei, palmar and dorsal, devoted to the purpose of lateralizing the digits, the first series being flexors, and the second being extensors. In the typical limb, where each digit has a vital individuality of action, we should expect to find these muscles characteristically and perfectly developed; but as in the limbs of most vertebrates, when possessing four or five digits, only one or at most two of them maintain this separateness of action, in the intermediate segments consolidation of the metacarpals or metatarsals interferes with independency of action; still we find

the uniformity of development of the typical muscle-germs distinctly traceable. It must at once be noticed that the interossei of the human hand and human foot do not correspond, but differ strikingly in respect to their line of action—those of the manus working to and from the line of the middle finger, those of the pes having a similar relation to the second toe. In the pes of the chimpanzee, Humphry has found them arranged in the same way as we find in the human manus. In the gorilla, Duvernoy and Halford found them to be arranged in the same manner; and the latter anatomist has met with the same arrangement in *Macacus*. I have examined them in *Cercopithecus*, *Macacus*, *Rhesus*, and *Cynocephalus*; and Mivart has examined the first-named genus, and found them alike. Prof. Humphry has dissected them in the dog, and has found the same arrangement, which I have likewise confirmed, in a dingo. In the manus of *Dasypus* I have found them arranged thus:—the fifth digit had an internal interosseus from the carpus to the first phalanx; the fourth had none; the third had a fasciculus attached to its ulnar side; the second had a special one to its radial side; and the pollex had one to each side. Thus we see another instance of a variation from the true manus type. But it is in *Ornithorhynchus*, *Hyrax*, and *Nycticebus* that these attain their greatest degree of complexity. In the first named a regular double set of muscles occupy the interosseous spaces, one for each side of each finger. In *Hyrax* there are two sets of interosseals:—first, a regular set, one at each side of each finger, and inserted into the sesamoid bones at the base of the first phalanges; secondly, a group of longer muscles—one an external muscle for the index, two external parallel muscles for the annularis, and one for the little finger, supplemented by an abductor minimi digiti. In the foot of this animal there are internal and external muscles for the index, middle, and fourth toes, an external muscle for the third, and of the longer series an inner tendon for the third, and external muscles for the second and first. The *Nycticebus* likewise possesses a complex group of interossei as well as of lumbricales, as in its manus are found an abductor and flexor brevis pollicis, external and internal interossei for the index, middle, annular, and little digits, supplemented by a special abductor of the latter and by a transversus pedis consisting of two slips, one springing from the second and the other from the third metacarpal bone. The rat and hare possess four pairs, as also does the rabbit; while the guineapig and *Agouti* exhibit three pairs of interossei.

In deducing from these apparently dissimilar series a regular typical form we see that the entire difficulty may be set at rest

by the assumption that for the typical digit there are four such muscles—a palmar on each side and a dorsal on each side. In the human manus, which we will take for illustration as the most familiar, we have these developed as follows. The pollex on its free side has a muscle, the abductor, which, however, is generally divisible into two, an abductor exterior and interior, so named by Sömmerring. The interior of these, undoubtedly, acts (as Meckel suggests) as a palmar interosseus; this muscle is present in *Ornithorhynchus*, in the opossum, in the bear, *Gulo*, and others. On its ulnar side a muscle is occasionally present as an anomaly in man, described by Henle—the interosseus primus volaris, which I have never found as a portion of the normal anatomy of any animal. Meckel, however, in speaking of the short muscles of the thumb, says:—"Il y a quelquefois, par exemple chez le magot, un petit fléchisseur plus profond que l'on rencontre parfois aussi dans l'homme." This might perhaps be the muscle of Henle; and Prof. Huxley has described it as existing in the gorilla (Med. Times & Gazette, 1864, p. 538). For the index finger there is a radial palmar muscle, which in the human subject arises from the os magnum and the base of the third metacarpal; but as its function as a radial lateralizer of the index is better fulfilled by one of the dorsal muscles, its insertion is shifted to the inner sesamoid bone of the pollex, and it becomes the deep head of the flexor pollicis. I have found this muscle in *Hystrix cristata*; and, as stated above, in *Dasypus* this muscle is present and typical, attached to the radial side of the index. The palmar ulnar interosseus is developed as the first palmar interosseus of the human hand. It is present in the pes of many monkeys, of the dog, and the *Ornithorhynchus*. For the middle finger the two palmar interossei, being superseded in function by the dorsals, would be entirely atrophied, but that they are devoted to a special purpose; and hence, coalescing, they are inserted into the inner sesamoid bone of the pollex, constituting the adductor pollicis. In the dog this muscle is represented by a fibrous band, not truly muscular; it is muscular, however, in *Ursus arctos*; and in some monkeys (as *Macacus nemestrinus*) it is large; in *Ursus* a slip of it is occasionally inserted into the second toe at its base, constituting a special adductor indicis. *Nycticebus* presents us with the intermediate state of this muscle, between the foot arrangement, to be referred to presently, and the typical human arrangement; for in this animal the accomplished anatomists who have given us so complete a monograph upon its myology have described, besides the typical interossei, fine fasciculi arising from the third and fourth metacarpals and inserted into

the pollex: these are differentiated fasciculi of the muscles utilized for an important special purpose.

The annularis or ring-finger has in man its palmar radial muscle developed as the second palmar interosseus; and the palmar ulnar, which arises generally from the unciform bone, is shifted in its insertion, into the first phalanx of the little finger, and constitutes the flexor brevis minimi digiti. For the little finger the radial palmar muscle is developed in man and the quadrumana as the third palmar interosseus; and as such it exists in the armadillo. The palmar ulnar muscle is developed into an abductor minimi digiti in the human hand: this fact was first noticed in the case of the *Ornithorhynchus*, by Meckel; but it will be found equally true in man, the cat, and in such of the quadrumana as I have examined.

The pedes of vertebrate animals, both mammalian and reptilian, exhibit a corresponding series of muscles. Taking the human foot as an example, we find for the tibial side of the hallux a muscle, the abductor pollicis, or at least its calcanean head, which is found in quadrumana, many carnivora, and marsupialia. On the fibular side a corresponding muscle, the flexor brevis pollicis, occurs, a muscle whose single origin indicates that it is not the complete representative of its synonym in the hand. This muscle is absent in some monkeys, as the mandril, but large in others, as *Macacus*. The second toe has its tibial muscle circumstanced like its fellow of the manus, and is thus modified into the adductor hallucis, a muscle which is the undoubted representative of the deep head of the hand flexor. From the fibular side of the second metatarsal we find what should be the outer of the plantar muscles modified into the first slip of the musculus transversus pedis, and crossing the metatarsal bone to be inserted into the outer sesamoid bone of the hallux; the remainder of this transversus is made up of the fibular interossei of the third, fourth, and part of the fifth uniting and running transversely: its obvious manus representative is the adductor pollicis, to which there is very often an accessory fasciculus from the fourth metacarpal superadded, as noticed by Huxley (*loc. cit.* p. 538). The tibial interosseus of the third, fourth, and fifth toes remain in man unchanged, as the first, second, and third plantar interossei respectively; of these the two last named exist in *Cercopithecus* and *Macacus*, but the first in these animals is either prolonged as a rudiment of the transversus pedis or absent altogether. The flexor brevis minimi digiti is made up of the remainder of the last fibular muscle that is not required for the transversus.

The plantar interossei having thus been accounted for in man, it only remains to refer to their types the muscles in those

animals already noticed as instances of a greater degree of complexity than usual—the *Hyrax*, *Nycticebus*, &c.; and in all these we merely see approximation to the true type, in various degrees of distinctness. The long muscles in *Hyrax* are probably displaced dorsal interossei, and the short interphalangeal muscles of *Nycticebus* may belong to the same type.

The last class of muscles in the manus which are specially devoted to produce the movements of the digits is that of the dorsal interossei. These we usually find to be bicipital; and accepting this appearance as an evidence of the coalescence of two muscle-germs, we can easily allocate these muscles to their respective places. As extension is a much simpler act than flexion, the latter being liable to endless modifications in grasping, &c., so extensor muscles are much less disposed to vary than flexors. Taking, again, the hand of man as an example, we find the radial dorsal muscle of the pollex present as the abductor pollicis exterior of Sömmerring. The ulnar dorsal muscle constitutes the polliceal origin of the first dorsal interosseus, whose thumb insertion is obsolete. For the index finger the radial dorsal muscle is developed as the first dorsal interosseus; this muscle in *Macacus nemestrinus* has no polliceal; but it is bicipital in *Simia* and in the hyæna and dog. The ulnar dorsal muscle constitutes the outer head of the second interosseus. For the middle finger the dorsal radial muscle forms the medial head of the second dorsal interosseus, and the ulnar makes the corresponding head of the third dorsal of the human hand. In the ring-finger the radial muscle is modified into the annular origin of the third dorsal interosseus, and the ulnar constitutes the annular origin of the fourth. For the little finger the radial muscle forms the ulnar head of the fourth dorsal interosseus, and the ulnar forms the opponens minimi digiti.

The pes exhibits an equally regular series. For the hallux the dorsal tibial muscle is developed as the second head of the abductor pollicis, and the dorsal fibular as the inner head of the first dorsal interosseus. The second toe has its tibial muscle in the form of the outer head of the first external interosseus, and its fibular as the inner head of the second dorsal: this muscle differs from its fellow in the manus in being inserted into the second instead of the third finger. For the third toe the tibial muscle constitutes part of the second dorsal interosseus, and the fibular that part of the third which is attached to the third metatarsal bone. Similarly the two dorsal muscles for the fourth toe constitute respectively parts of the third and fourth external interossei. For the little toe the tibial muscle

forms the second head of the fourth dorsal, while the fibular constitutes the abductor minimi digiti.

Thus we find that all the muscles of the manus and pes may be reduced into a regular ordinal series. The only supplemental muscles to these are the lateralizers of the metacarpals, of which two are usually present:—one an opponens of the metacarpal of the thumb, often present as an accidental variety in the pes; and secondly the lateralizer of the fifth metatarsal bone, present in the foot as the "abductor ossis metacarpi quinti" muscle of Wood, Huxley, and Flower. Perhaps there may be a complete series of these in a typical limb; but I am not aware of any others being present in any individual animal.

XL.—*Descriptions of two New Species of Humming-birds.*

By John Gould, Esq., F.R.S.

Eriocnemis smaragdinipectus.

Head and upper surface dullish grass-green; rump and upper tail-coverts resplendently luminous yellowish green; on the throat a patch of violet-blue; thence to the vent glittering grass-green; under tail-coverts bright blue; thighs thickly clothed with white downy feathers; bill, primaries, and tail-feathers black.

Total length 4 inches, bill $\frac{15}{16}$, wing $2\frac{5}{16}$, tail $1\frac{5}{8}$.

Hab. Ecuador.

Remark.—This species, which is from the neighbourhood of Quito, is very closely allied to *Eriocnemis vestita*, but differs from that bird in the green of the breast commencing immediately below the blue throat-spot, whereas in fine old males of *E. vestita*, when viewed in bright sunlight, a black band is seen separating the two colours. It is true that this band is green in certain lights; but the feathers are of a different structure to those of the Quitan species. Taking the average of seven specimens of both kinds, I find the *E. smaragdinipectus* has a rather longer bill and somewhat shorter wing than the *E. vestita*; in all other respects their dimensions are very similar. The green of the abdomen of the former is more pure, or not so yellow as the same part of the latter; in the gorgeous colouring of the rump perhaps the Quitan bird is somewhat less resplendent than the Bogotan *E. vestita*. I have ample materials at my disposal for determining the distinctness of the two birds; and, however similar they may be, there are sufficient tangible characters by which each may be recognized, and to show that they are really different.